PRESENT STATUS AND PROBLEMS OF BAMBOO CLASSIFICATION *

D. GROSSER AND W. LIESE

STATUS OF BAMBOO CLASSIFICATION

THE FIRST BAMBOO CLASSIFICATION originates from Rumpf (1750) who divided the bamboos into 8 classes, all with the name *Arundo*. This classification system was used with little change by Linné (1753), Roxburgh (1814), and Ruprecht (1839), until Munro (1868) proposed his new system which is still applied in principle today. Bentham (1883) modified the system of Munro so that instead of three divisions (Triglossae (Arundinarae), Bambuseae verae, and Bacciferae) four subtribes were introduced. Hackel (1889) and Gamble (1896) adopted the system of Bentham unchanged. It is represented by the following arrangement:

CLASSIFICATION SYSTEM OF BENTHAM (1883)
[Including genera added by Hackel (1889) and Gamble (1896)]

Subtribe 1
Arundinarieae: Stamens usually 3, palea 2-keeled. Pericarp thin, adnate to the seed.
GENERA: *Arundinaria*, *Arthrostylidium*, *Phyllostachys*, *Athroostachys*, *Merostachys*, *Chusquea*, *Planotia*

Subtribe 2
Eubambuseae: Stamens 6, palea usually 2-keeled. Pericarp thin, adnate to the seed.
GENERA: *Nastus*, *Guadua*, *Bambusa*, *Thyrsostachys*, *Guaduella*, *Atractocarpa*, *Gigantochloa*, *Oxytenanthera*, *Puelia*

Subtribe 3
Dendrocalameae: Stamens 6, palea 2-keeled. Pericarp fleshy or crustaceous, separable from the seed.
GENERA: *Dendrocalamus*, *Melocalamus*, *Pseudostachyum*, *Teinostachyum*, *Greslania*, *Cephalostachyum*

Subtribe 4
Melocanneae: Stamens 6 or more, spikelets 1-flowered; palea none or similar to the flowering glume. Pericarp crustaceous or fleshy, separable from the seed.
GENERA: *Schizostachyum*, *Dinochloa*, *Melocanna*, *Ochlandra*.

* This investigation was supported by the Deutsche Forschungsgemeinschaft.

Slight modifications to the system of Bentham were made by E. G. Camus (1913) and by Stapf (1917). Camus arranged the genera in five tribes and four subtribes while Stapf combined the African genera *Puelia*, *Guaduella* and *Atractocarpa* of the second subtribe into a separate fifth subtribe (Pueliinae). The system of Stapf was adopted by Hubbard (1934) in Hutchinson's monograph "Monocotyledons." A markedly different system was proposed by A. Camus (1935) as an expansion of the system formulated by her father E. G. Camus (1913). She assigned all genera having filaments united to form a tube into a special tribe Synandrae, resulting in a total of seven tribes and four subtribes.

CLASSIFICATION SYSTEM OF A. CAMUS (1935)

	GENERA
Tribus I Arundinariae:	*Sasa, Oreiostachys, Arundinaria, Thamnocalamus, Fargesia, Phyllostachys, Microcalamus, Glaziophyton*
Tribus II Arthrostylideae:	*Arthrostylidium, Aulonemia, Merostachys*
Tribus III Chusqueae:	*Chusquea, Planotia*
Tribus IV Bambuseae verae:	*Guadua, Guaduella, Bambusa, Oreobambus, Nastus, Greslania, Thyrsostachys*
Tribus V Hickelieae:	*Hickelia*
Tribus VI Synandrae:	*Puelia, Atractocarpa, Gigantochloa, Oxytenanthera, Neohouzeaua*
Tribus VII Baccifereae	
Subtribus I Dendrocalaminae:	*Pseudostachyum, Teinostachyum, Dendrocalamus, Cephalostachyum, Melocalamus*
Subtribus II Melocanninae:	*Schizostachyum, Dinochloa, Melocanna, Ochlandra*
Subtribus III Pseudocoixinae:	*Pseudocoix.*
Subtribus IV Perrierbambusinae:	*Perrierbambus.*

Holttum (1946, 1956) regarded the tribe Synandrae of A. Camus as unnatural. In his opinion, the main differences between Bentham's subtribes, based on fruit-structure, are not in accordance with the observed natural characters. Although fruit structure is considered of basic importance by Munro (1868) and Bentham (1883), both studied only very few fruits and their limited observations were insufficient for the weight given them in their system. Furthermore, they neglected the structure of the ovary, the spikelet (except in the fourth subtribe), and the inflorescence. As a result, a thorough revision of bamboo classification was considered necessary by Holttum (1956). As the basis for a natural classification he proposed a new system based on the structure of the ovary. In comparison with earlier systems it contains substantial changes within the four divisions to which the genera have been assigned.

CLASSIFICATION SYSTEM OF HOLTTUM (1956)

A. Schizostachyum type of ovary:
Melocanna, *Ochlandra*, *Schizostachyum* (including *Teinostachyum*, *Pseudostachyum*, *Cephalostachyum*, and *Neohouzeaua*).

B. Oxytenanthera type of ovary:
Oxytenanthera (sensu stricto).

C. Bambusa-Dendrocalamus type of ovary:
Melocalamus, *Dinochloa*, *Thyrsostachys*, *Bambusa*, *Guadua*, *Dendrocalamus*, *Gigantochloa*, *Racemobambos* (including *Chloothamnus*).

D. Arundinaria type of ovary.

There is hardly any other group of flowering plants so difficult to identify and classify as are the bamboos. This is mainly because the common identification based on flowers and fruits is seldom possible since most bamboo species flower only at irregular intervals and often die soon after. There are also species which mostly remain sterile. For example, in *Bambusa vulgaris*, one of the most common species, only very few flowering specimens have been observed, and fruiting has never been seen (McClure, 1966). Only a few species flower annually or even constantly, e.g., *Arundinaria wightiana*, *Bambusa lineata*, *Ochlandra rheedii*, *O. stridula*, *Schizostachyum brachyladum*, *S. gracile* and *S. grande* (Gamble, 1896; Holttum, 1946; Raizada & Chatterji, 1956). Furthermore, the flowers of many tropical bamboo species undergo changes during their development so that their morphological characteristics vary according to the time of observation. The preparation of collected material is often difficult because the flowers are easily damaged. Misinterpretations are then possible, when new species or genera are described on the basis of such flower fragments in which essential floral characteristics may be missing (McClure, 1957a). Consequently, many species may be described under different names or members of the same species may be placed in different genera, or the same name may be given to quite different species.

As a result of these difficulties and uncertainties, a rather confused picture results. This is reflected not only in the classification systems mentioned above but also in the estimates of the numbers of species and genera, which vary from 500 to more than 1000 species, and from 30 to about 90 genera. Actually, the bamboos may contain around 600 to 700 species, excluding the bamboo grasses "Sasa" from Japan, which alone comprise 6 genera with more than 600 species. McClure (1957b), who concentrated in his first revision on 88 genera, which he had checked, later considered only 63 as "good," because he proved that several genera were described twice. The most important genera, together with the number of their species and their distribution, are listed in TABLE 1.

TABLE 1. **List of the more important bamboo genera with the number of their species and their distribution.**

GENERA	NUMBER OF SPECIES	DISTRIBUTION
ARTHROSTYLIDIUM Ruprecht	20	Central and South America
ARUNDINARIA Michaux	81	Asia, America, Africa
ATHROOSTACHYS Bentham	1	Brazil
ATRACTOCARPA Franchet	1	Congo
BAMBUSA Retzius corr. Schreber	73	Central and East Asia, Malaysia
BRACHYSTACHYUM Y. L. Keng	1	East Asia (China)
CEPHALOSTACHYUM Munro	9	India, Malaysia, Madagascar
CHIMONOBAMBUSA Makino	12	China, Japan, Korea, Taiwan
CHUSQUEA Kunth	71	Middle and South America
DENDROCALAMUS Nees	24	India–Philippines
DINOCHLOA Buse	9	Philippines, Java, Malaysia
FARGESIA Franchet	1–2	China
GIGANTOCHLOA Kurz ex Munro	12	India–Philippines
GUADUA Kunth	29	Middle and South America, Philippines
GUADUELLA Franchet	4	Central and West Africa
HICKELIA A. Camus	1	Madagascar
HITCHCOCKELLA A. Camus	1	Madagascar
INDOCALAMUS Nakai	7	China, Philippines
INDOSASA McClure		East Asia (China)
LELEBA** Nakai	(3)†	Japan
LINGNANIA McClure		China
MELOCALAMUS Bentham	1	India
MELOCANNA Trinius	2	India
MEROSTACHYS Sprengel	18	South America
NASTUS Jussieu	2–10	South America, Madagascar, Sumatra
NEOHOUZEAUA A. Camus	2	India, Indonesia, Laos
NEUROLEPIS Meisner	9	South America, New Guinea
NIPPONOBAMBUSA* Muroi	(12)†	Japan
OCHLANDRA Thwaites	11	Middle and East Asia, Malaysia, Ceylon, Madagascar
OREOBAMBUS K. Schumann	1	Africa (Usumbura)
OXYTENANTHERA Munro	16–18	Asia, New Guinea, Africa, Madagascar
PERRIERBAMBUS A. Camus	2	Madagascar
PHYLLOSTACHYS Siebold & Zuccarini	25	Japan, China, Taiwan, Indochina, Himalaya

PLEIOBLASTUS* Nakai	(93)†	China, Japan
PSEUDOCOIX A. Camus	1	Madagascar
PSEUDOSASA* Makino ex Nakai	4	Japan, Korea, China
PSEUDOSTACHYUM Munro	1–2	Himalaya (India)
PUELIA Franchet	1	West Africa, Congo, Gabon
RACEMOBAMBOS Holttum	5	Malaysia (Borneo)
SASA* Makino & Shibata	(400)†	Central and East Asia
SASAELLA* Makino	(132)†	Japan
SASAMORPHA* Nakai	(4)†	Japan, South China, Korea
SCHIZOSTACHYUM Nees	25	India–Philippines, Madagascar
SEMIARUNDINARIA Makino ex Nakai	(8–15)†	South China, Japan
SHIBATAEA Makino ex Nakai	1	China, Japan
SINARUNDINARIA Nakai		East Asia
SINOBAMBUSA Makino ex Nakai	(1)†	Japan
SINOCALAMUS McClure		China
TEINOSTACHYUM Munro	5	India, Ceylon
THYRSOSTACHYS Gamble	2	India, Thailand

* The genera in Japan called "SASA" comprise more than 600 species; they are distinguished from the group of bamboo species called "TAKE."

Division of the Bambusaceae in Japan

GENERA OF BAMBOO GRASS ("SASA")	GENERA OF BAMBOO ("TAKE")
Nipponobambusa	*Leleba***
Pleioblastus	*Phyllostachys*
Pseudosasa	*Semiarundinaria*
Sasa	*Sinobambusa*
Sasaella	*Chimonobambusa* (including *Tetragonocalamus*)
Sasamorpha	*Shibataea*

** In Japan all *Bambusa* species with thorny branches are combined in *Leleba*.
† The numbers of species growing in Japan. Sources: Raizada & Chatterji (1956); McClure (1957b); Ueda (1960); Prat (1960); Hino (1961); and Lin (1967).

Because the flowers of many bamboos appear only infrequently, special importance has to be given to the vegetative structures, too. A comprehensive description of the morphology of the vegetative parts of the bamboos is given by Holttum (1958) in his taxonomic account of the bamboos of the Malay Peninsula together with a key to these species based on vegetative characters. Of special value as diagnostic characters are the culm sheaths, which have been investigated in detail by Chatterji & Raizada (1963). Their description and key to the identification of 22 Indian bamboo species is, however, not satisfactory, since no distinctions were made between the ligule and the auricles (Holttum 1972). The key itself is rather restricted in its application because of considerable variations within the same species and an overlapping between different species and genera (Pattanath & Ramesh Rao, 1969). Furthermore, it can be used only for sheaths of mature culms, because in immature ones differences in shape, size, and texture of the sheaths may occur. It is also necessary to recognize that culm sheaths, leafy twigs, and other vegetative structures alone are not satisfactory substitutes for herbarium material of flowering specimens, in spite of their usefulness for identification purposes. Holttum (1972) pointed out that he could not define any genus on vegetative characters only. However, the collection and study of individual bamboos cannot be deferred until they are flowering.

Therefore, McClure (1957a, 1966) proposed that at first a complete description of the vegetative structures of sterile bamboos should be made and the description of the reproductive structures should be added after flowering has been observed. These suggestions appear all the more important, since during flowering culm growth is more or less reduced, so that no new culms with sheaths are produced and the older sheaths soon disappear. This is why culm sheaths and flowers of the same plant are only rarely present together in herbaria.

Classification Based on Anatomical Characters

Intensive investigations were carried out on 52 species of bamboo in 14 genera, collected in India, Bangla Desh, Thailand, Indonesia, the Philippines, Taiwan, and Japan, which are listed in detail by Grosser (1971) in his contribution to the histology and classification of Asian bamboo species. The results have revealed that the anatomical characters of the bamboo culms are of considerable value for taxonomic identification, since distinct differences in the structure of the vascular bundles exist between various genera as well as between many species. For most of the species investigated a characteristic shape, size, and arrangement of the vascular bundles could be demonstrated, on the basis of which an anatomical classification system has been devised, which is discussed in the following section.

In order to understand the principles of this system the anatomical structure of bamboo culms must be described briefly (for details see Grosser, 1971; Grosser & Liese, 1971; Grosser & Zamuco, 1971).

The anatomical structure of bamboo culms is mainly determined by the collateral vascular bundles embedded in the parenchymatous tissue. The vascular bundles are small, numerous and close to each other near the periphery, becoming larger and more widely distributed towards the center of the culm. However, in the inner culm of plants of many species the bundles appear smaller again. Consequently, they reach their maximum size in the central zone where they also exhibit their characteristic form (FIGURE 1). The phloem and xylem part of each bundle is surrounded by sclerenchymatous sheaths, differing in size and shape according to their position within the culm of the given bamboo species. Each vascular bundle in the central zone possesses four of these sheaths; two lateral on either side of the vessels, and two polar, surrounding the phloem

FIGURE 1. *Dendrocalamus giganteus* Munro. Cross section of culm wall, a, outer, b, middle, c, inner part of the culm, all, × 11.


a
b
c

and the intercellular space. Additionally, many genera possess isolated fiber strands, situated either only on the inner side of the vascular bundle or on the inner and outer sides; they are separated from the central vascular strand by a few rows of parenchyma cells. Consequently, two structural types of arrangement of the supporting tissue can be distinguished: sheaths and strands. Bamboo species with isolated fiber strands, therefore, possess vascular bundles consisting of two or even three parts, depending on whether one or two fiber bundles are present in addition to the central vascular strand. On the other hand, bamboo species with only sclerenchyma sheaths have vascular bundles consisting of only one part. Depending on the presence or absence of these types of vascular structures, four basic vascular bundle types can be distinguished. These are described in detail in TABLE 2 and illustrated in FIGURES 2, 3, 4, and 5.

TABLE 2. **Basic vascular bundle types in bamboos** (from Grosser & Liese 1971)*

Vascular bundle type I (a)

CHARACTERISTICS: Consisting of one part (central vascular strand); supporting tissue only as sclerenchyma sheaths; intercellular space with tyloses.

OCCURRENCE: In all species with leptomorph rhizomes throughout the culm as the only type (*Arundinaria, Phyllostachys*). See FIGURE 2.

Vascular bundle type II (b)

CHARACTERISTICS: Consisting of one part (central vascular strand): supporting tissue only as sclerenchyma sheaths; sheath at the intercellular space (protoxylem) strikingly larger than the other ones; intercellular space without tyloses.

OCCURRENCE: In species with pachymorph rhizomes growing either in single-culm-formation (*Melocanna*) or in clumps (*Cephalostachyum, Schizostachyum, Teinostachyum*). In *Cephalostachyum* as the only type throughout the culm; in *Melocanna, Schizostachyum, Teinostachyum* in the basal internodes often together with type III. See FIGURE 3.

Vascular bundle type III (c)

CHARACTERISTICS: Consisting of two parts (central vascular strand and one fiber strand); fiber strand inside the central strand; sheath at the intercellular space (protoxylem) generally smaller than the others.

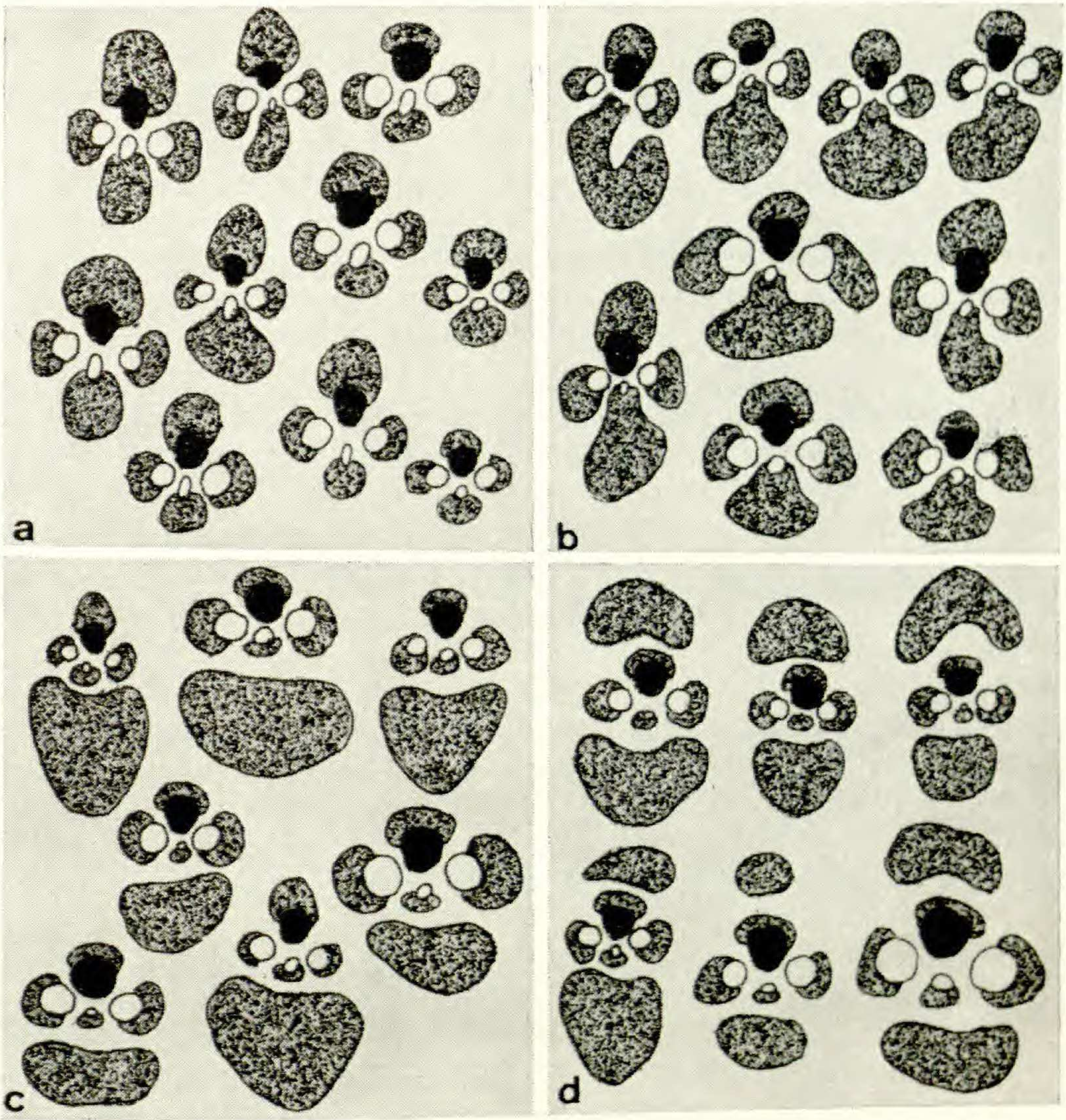
OCCURRENCE: In clump-forming species with pachymorph rhizomes (*Bambusa, Dendrocalamus, Gigantochloa, Thyrsostachys*); at the basal internodes combined mostly with type IV, in the middle and upper parts as the only type. In *Melocanna, Schizostachyum,* and *Teinostachyum* combined at the basal internodes with type II. In some *Oxytenanthera* species, as the only type throughout the culm. See FIGURE 4.

Vascular bundle type IV (d)

CHARACTERISTICS: Consisting of three parts (central vascular strand and two fiber strands); fiber strands outside and inside the central strand.

OCCURRENCE: In clump-forming species with pachymorph rhizomes (*Bambusa, Dendrocalamus, Gigantochloa, Thyrsostachys*): mostly at the basal internodes, seldom at the middle part; always combined with type III. See FIGURE 5.

*TABLE 2 (text and illustrations) from Grosser & Liese 1971, reproduced here by permission of Springer-Verlag, Berlin.



Based on the presence of these four basic types as well as combinations of them within one culm, an anatomical system of classification can be drawn up. It consists of four main groups, one of which is divided into two sub-groups:

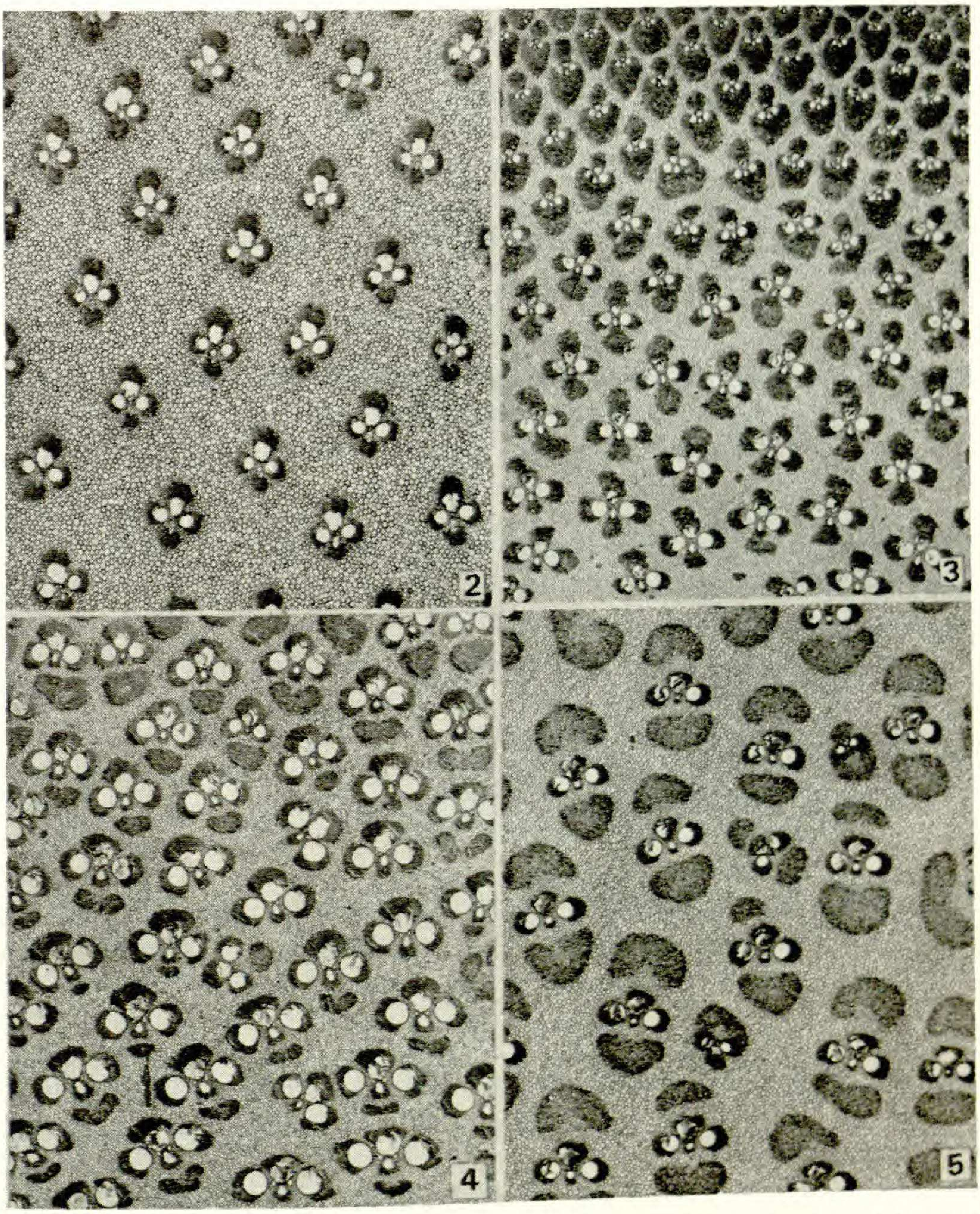
GROUP A	Genera having vascular bundle type I consisting of one part: *Arundinaria, Phyllostachys, Tetragonocalamus.*
GROUP B	Genera having vascular bundle type II consisting of one part.
GROUP B 1	Genera having type II alone: *Cephalostachyum.*
GROUP B 2	Genera having type II combined with type III, consisting of two parts: *Melocanna, Schizostachyum, Teinostachyum.*
GROUP C	Genera having vascular bundle type III consisting of two parts alone: *Oxytenanthera.*
GROUP D	Genera having type III, consisting of two parts combined with type IV consisting of three parts: *Bambusa, Dendrocalamus, Gigantochloa, Thyrsostachys.*

GROUP A with the vascular bundle type I consisting of one part, in general characterizes the leptomorph genera which are growing monopodially, whereas the pachymorph genera with sympodial growth are typified by the GROUPS B, C, and D with the vascular bundle types II, III, and IV, consisting of one, two, and three parts respectively (see TABLE 2). Between these two morphologically different bamboo groups there also exist distinct structural differences. As far as the distribution of genera is concerned, our classification system based on vascular bundle types is in accordance to a large extent with Holttum's (1956) which is based on similarities in reproductive structures. The anatomical results confirm Holttum's opinion that neither the widely applied system of Munro modified by Bentham (1883), nor the system by A. Camus (1935) agrees with the natural order.

The genera *Bambusa* and *Dendrocalamus*, which in the older classifications have been placed for nearly a century in different subtribes or tribes, possess very similar anatomical structures. Pattanath & Ramesh Rao (1969) also noted that both genera have several anatomical features in common. Therefore, both genera should be grouped together as Holttum also proposed. Furthermore, on the basis of their vascular bundles the genera *Gigantochloa* and *Thyrsostachys* belong to the Bambusa-Dendrocalamus-GROUP D. On the other hand, *Dendrocalamus* has a distinctly different structure from *Teinostachyum* and *Cephalostachyum* so that these two genera cannot be placed together with *Dendrocalamus* in one group as was formerly done, but rather into different groups as suggested by Holttum. The *Teinostachyum* and *Schizostachyum* species investigated have such a similar structure that Holttum's proposal to include the *Teinostachyum* species in the genus *Schizostachyum* would conform with the natural order. The extent to which this also applies to *Pseudostachyum* and *Neohouzeaua* has not so far been determined anatomically. However, in contrast to the proposal of Holttum, the genus *Cephalostachyum* appears to be anatomically less related to the genus *Schizostachyum* so that its inclusion in the latter should be examined further.

The genus *Melocanna* belongs to GROUP B, together with the genera *Cephalostachyum* and *Schizostachyum* including *Teinostachyum*. It shows, however, more similarities with *Schizostachyum* than with *Cephalostachyum*. All four genera possess the vascular bundle type II which is present either alone (*Cephalostachyum*) or in combination with type III (*Melocanna*, *Schizostachyum* and *Teinostachyum*) so that two SUBGROUPS, B 1 and B 2, can be distinguished.

The genus *Oxytenanthera* forms a separate group, both on the basis of its morphology in the system of Holttum as well as from the anatomical point of view. Holttum (1956) shows that *Oxytenanthera* species from Asia described by Munro & Gamble are either species of *Dendrocalamus* or species of *Gigantochloa* and concludes that the genus *Oxytenanthera* is exclusively African. Consequently, his "group B — ovary of the Oxytenanthera type" should be restricted to the African species (type species *O. abyssinica* (A. Richard) Munro). In fact *O. nigrociliata* Munro from



FIGURES 2–5, illustrating basic vascular bundle types I–IV, all from 6th internode, × 16. 2, *Phyllostachys edulis* Riv., type I; 3, *Cephalostachyum pergracile* Munro, type II; 4, *Oxytenanthera albociliata* Munro, type III; 5, *Bambusa polymorpha* Munro, type IV.

FIGURES 2–5, from Grosser & Liese 1971, reproduced here by permission of Springer-Verlag, Berlin.

Asia has a vascular bundle type structure closely related to the *Dendrocalamus* and *Gigantochloa* species, which would confirm Holttum, who placed *O. nigrociliata* in *Gigantochloa*. However, two other species of this genus, *O. albociliata* Munro and *O. hosseusii* Pilger, exhibit distinct differences from *Dendrocalamus* and *Gigantochloa* (Grosser, 1971; Grosser & Liese, 1971). The same differing structure probably occurs in the

African *O. abyssinica* as can be concluded from investigations of a few basal internodes obtained from Sudan. Pattanath & Ramesh Rao (1969) also indicate a vascular bundle structure for basal internodes of *O. abyssinica* which appears to be similar to that of *Oxytenanthera albociliata*.

At least some species of *Oxytenanthera* growing in Asia probably possess an anatomical structure closely related to *Oxytenanthera abyssinica*. However, only a thorough investigation of their morphology, especially of the reproductive structures, and the histology of the genus will clarify which of the 16 to 18 species of *Oxytenanthera* described so far belong to the genus *Oxytenanthera* sensu Holttum, and those which must be included in the genera *Dendrocalamus* and *Gigantochloa*. Holttum (1972) points out that his assessment of the distinctiveness of the ovary characters of *O. abyssinica* was possibly wrong and that these observations need a re-analysis. Therefore *O. abyssinica* (type species) might be more closely related to *Dendrocalamus* than was previously thought. Otherwise, two anatomical groups could be differentiated: one closely corresponding to *Dendrocalamus* and *Gigantochloa* (e.g., *O. nigrociliata*, placed in *Gigantochloa* by Holttum), and the other not corresponding to these genera (e.g., *O. abyssinica*, *O. hosseusii* and *O. albociliata*, the last one placed in *Dendrocalamus* by Holttum).

At first glance, a revision appears necessary for *Dendrocalamus membranaceus* Munro because the anatomy of this species, collected in the Botanical Garden of the Forest Research Institute, Dehra Dun (India), differs considerably from the other eight *Dendrocalamus* species investigated so far, but resembles markedly *O. albociliata*. Its affinity to the genus *Dendrocalamus*, therefore, appears questionable from the histological viewpoint. More likely this species belongs to *Oxytenanthera*. Parker (see Chatterji & Raizada, 1963) assumed on morphological evidence that *D. membranaceus* Munro and *Oxytenanthera lacei* Gamble are identical. But Holttum (1972) definitely regards *D. membranaceus* as a species of *Dendrocalamus*; it has short spikelets with 2 or 3 perfect florets, much like those of *Dendrocalamus strictus* (Roxb.) Nees, the type species of the genus. Therefore the culms collected as *D. membranaceus* in Dehra Dun may in fact belong to another species. An anatomical comparison with plants from other botanical gardens appears necessary to obtain conclusive results.

In cases where the thickness of the culm wall is insufficient (e.g., *Bambusa multiplex* (Lour.) Raeusch, a species with only small thin-walled culms) the vascular bundle type IV with its three parts appears only rarely in internodes near the ground. Also in other *Bambusa* and *Dendrocalamus* species vascular bundles of the basic type IV may not be developed if the culm remains small and thin-walled because of unsuitable growing conditions. For the formation of vascular bundle type IV, the culm wall must have a thickness of at least 10–25 mm., according to the species. Consequently, species belonging to the GROUP D may have vascular bundle types of the GROUP C in their smaller culms. For the pachymorph genera a classification into four different culm types has been described inyolving three vascular bundle types: B (divided into B1 and B2), C, and D. In contrast, all leptomorph genera have the same vascular bundle type, represented by GROUP A. Consequently, not only species of the genera *Arundinaria*, *Phyllostachys* and *Tetragonocalamus* investigated by the authors (Grosser, 1971; Grosser & Liese, 1971) but also leptomorph species of the genera *Brachystachyum*, *Chimonobambusa*, *Indocalamus*, *Phyllostachys*, *Pleioblastus*, *Pseudosasa*, *Semiarundinaria*, *Sinobambusa*, and *Shibataea* (investigated by Li & Chin, 1960; and by Li, Chin & Yao, 1962) possess these types of vascular bundles. The Chinese authors have grouped the 24 species from 14 genera investigated into 15 different culm types, designated as different anatomical groups. They have chosen for their anatomical characterization the vascular bundle sequences from internodes of the middle of the culm. Such sequences consist of the radial order of vascular bundles across the culm-wall from the periphery towards the center. However, form, size, and distribution of the vascular bundles vary considerably across the culm-wall. Furthermore, each bamboo species has a more or less typical sequence of vascular bundles. Thus, their classification system is rather complex leading to 15 different types for only 24 species; the conformity of species related to each other becomes unclear. Also, the system refers only to the internodes from the middle part of the culm, whereas the vascular bundles and their sequences vary considerably in height position within one culm (Grosser, 1971; Grosser & Liese, 1971). Therefore, the classification system by Li, Chin & Yao (1960, 1962) cannot be regarded as representative either for the whole culm or for the species itself.

CONCLUSIONS

The results of our anatomical investigations on 52 bamboo species of 14 genera clearly demonstrate that for the classification of species and genera into natural systematic groups not only the morphology of the reproductive structures can be used, but also anatomical characters, in particular the structure of the vascular bundles. Because many bamboo species flower only rarely, classification systems based solely on reproductive characters, such as those of Munro (1868), Bentham (1883), Gamble (1896), E. G. Camus (1913), A. Camus (1935), and Holttum (1956) have limited value for the identification of standing culms. Similarly, morphological features of vegetative organs such as culm sheaths, are suitable for identification purposes only to a limited extent because of their variation in the same species, and their overlapping between species and genera. Additionally they are absent in culms cut for use. Other morphological features like the habit of the culms, the number and length of internodes, wall thickness, etc. are by themselves only of restricted diagnostic value. Consequently, more emphasis should be placed on anatomical structure, because significant anatomical differences exist between species of a genus and between genera. These differences can be applied successfully for the designation of bamboo genera into natural systematic units and for the further development of a modern bamboo classification. For a system of identification of bamboos — to be more independent of any one morphological state (e.g., sterile, flowering, cut, converted) — it is suggested that the following approach should be adopted:

A. Consideration of the *morphology of reproductive structures* — according to Holttum's classification.
B. Consideration of the *morphology of all important vegetative organs* — according to the results of Holttum (1958) and Chatterji & Raizada (1963) and the proposals of McClure (1957a, 1966).
C. Consideration of *anatomical characters of the culms* — according to the vascular bundle types described above (Grosser & Liese, 1971) and the results of study of the epidermal structure by Ghosh & Negi (1960) and Pattanath & Ramesh Rao (1969).

SUMMARY

In the present paper the current status and problems of bamboo classification are discussed. Comparative histological investigations on 52 bamboo species from 14 genera, collected in seven Asian countries, have shown that certain anatomical features of the culm are of taxonomic value. They can be used successfully in addition to morphological characters of the reproductive and vegetative organs for the differentiation of bamboo into natural systematic units. The classification system presented is based on four vascular bundle types and combinations of them within one culm. This system coincides to a large extent with the classification of Holttum based on the structure of the ovary. Both the systems as well as the older classifications are discussed.

REFERENCES

BENTHAM, G. Gramineae. IN: BENTHAM, G., & J. D. HOOKER. Genera Plantarum. 3(2): [Bambuseae] 1076, 1077; 1094–1096; 1207–1215. 1883. London. Reeve.

CAMUS, A. Classification des Bambusées. Arch. Mus. Hist. Nat. Paris. Sér. 6. **12:** 601–605. 1935.

CAMUS, E. G. Les Bambusées: monographie, biologie, culture, principaux usages. 1913. Paris. Paul Lechevalier, 215 pp.

CHATTERJI, R. N., & M. B. RAIZADA. Culm-sheaths as an aid to identification of bamboos. Indian Forester **89:** 744–756. 1963.

GAMBLE, J. S. The Bambuseae of British India. Ann. Roy. Bot. Gard. Calcutta **7:** xvii + 133 pp. 1896. Reprinted by Willmer Brothers, Ltd. Birkenhead, England. 1966.

GHOSH, S. S., & B. S. NEGI. Anatomy of Indian bamboos. Part I. Epidermal features of *Bambusa arundinacea* Willd., *B. polymorpha* Munro, *B. vulgaris* Schrad., *Dendrocalamus membranaceus* Munro, *D. strictus* Nees and *Melocanna bambusoides* Trin. Indian Forester **86:** 719–727. 1960.

GROSSER, D. Beitrag zur Histologie und Klassifikation asiatischer Bambusarten. Mitt. Bundesforschungsanstalt Forst- und Holzwirtschaft, Reinbek, Nr. 85. 321 pp. *pls. 1–23.* 1971.

——— & W. LIESE. On the anatomy of Asian bamboos, with special reference to their vascular bundles. Wood Sci. Technol. **5**(4): 290–312. 1971.

——— & G. I. T. ZAMUCO, JR. Anatomy of some bamboo species in the Philippines. Philippine Jour. Sci. **100**(1): [in press]. 1971.

HACKEL, E. Gramineae. IN: ENGLER, A., & K. PRANTL. Nat. Pflanzenfam. II. Abt. 2. [Bambuseae] 89–97. 1889. Leipzig. Engelmann.

HINO, I. Icones Fungorum Bambusicolorum Japonicorum. The Fuji Bamboo Garden. 335 pp. 1961.

HOLTTUM, R. E. The classification of Malayan bamboos. Jour. Arnold Arb. **27**: 340–346. 1946.

———. The classification of bamboos. Phytomorphology **6**: 73–90. 1956.

———. The bamboos of the Malayan Peninsula. Gard. Bull. Singapore **16**: 1–135. 1958.

———. Letter to Prof. Dr. W. Liese dated 16. Feb. 1972.

HUBBARD, C. E. Gramineae. IN: HUTCHINSON, J. The families of flowering plants. II. Monocotyledons. [Bambuseae] 203–205. 1934. Oxford.

LI, C.-L., & T.-C. CHIN. Anatomical studies of some Chinese bamboos. Acta Bot. Sin. **9**: 76–97. 1960.

———, ———, & H.-S. YAO. Further anatomical studies of some Chinese bamboos. Acta Bot. Sin. **10**: 15–28. 1962.

LIN, W.-C. The species and distribution of bamboos in the Republic of Malagasy (Madagascar). East African Spec. Bull. Taiwan For. Res. Inst. No. 4, 34 pp. 1967.

LINNÉ, C. VON: Species Plantarum. 1753.

MCCLURE, F. A. The taxonomic conquest of the bamboos with notes on their silvicultural status in the Americas. Paper presented to the 4th World Forestry Congress, Dehra Dun 1954. IN: Tropical Silviculture **2**: 304–308. 1957a. Rome.

———. Typification of the genera of the Bambusoideae. Taxon **6**: 199–210. 1957b.

———. The bamboos: a fresh perspective. Harvard Univ. Press, Cambridge, Mass. xv + 347 pp. 1966.

MUNRO, W. A monograph of the Bambusaceae. Trans. Linn. Soc. London. Bot. **26**: 1–157. 1868.

PATTANATH, P. G., & K. RAMESH RAO. Epidermal and internodal structure of the culm as an aid to identification and classification of bamboos. IN: Recent advances in the anatomy of tropical seed plants. Proc. 1st Nat. Symp. Muslim Univ. Aligarh. 179–196. 1969. Hindustan Publ. Corp. India.

PRAT, H. Vers une classification naturelle des Graminées. Bull. Soc. Bot. France **107**: 32–79. 1960.

RAIZADA, M. B., & R. N. CHATTERJI. World distribution of bamboo with special reference to the Indian species and their more important uses. Indian Forester **82**: 215–218. 1956.

ROXBURGH, W. Hortus Bengalensis. 1814.

RUMPF, G. E. Het Amboinsch Kruid-boek (Herbarium Amboinense). Amsterdam. 1750.

RUPRECHT, F. J. Bambuseas monographice expoint. Acad. St. Pétersburg. I–

XVIII. 1–71. 1839. Reprint: Bambuseae. Mem. Acad. St. Pétersb. (VI) Sci. Nat. 3(1): 91–165. 1840.

STAPF, O. System der Gramineae. IN: D. PRAIN, Fl. Trop. Africa **9**: 1917.

UEDA, K. Studies on the physiology of bamboo with reference to practical application. Bull. Kyoto Univ. Forests, No. 30. 167 pp. 1960.

DR. D. GROSSER
INSTITUT FÜR HOLZFORSCHUNG
UND HOLZTECHNIK
D–8 UNIVERSITÄT MÜNCHEN
WINZERERSTR. 45

PROF. DR. W. LIESE
INSTITUT FÜR HOLZBIOLOGIE UND
HOLZSCHUTZ DER BUNDESFORSCHUNGSANSTALT
FÜR FORST- UND HOLZWIRTSCHAFT
D-205 HAMBURG-LOHBRÜGGE
LEUSCHNERSTR. 91d